

Dynamic clams: changes in the bivalve fauna of Pacific islands as a result of sea-level fluctuations

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Abstract: Sea-level fluctuations continually alter the distribution and nature of shallow-water environments, although not all habitats are equally affected. Shallow-water habitats on coral reefs around oceanic islands can be divided into markedly different inner- and outer-reef systems. During regressions, the former are stranded while the latter persist. Previously I showed that numerous species are restricted to inner-reef habitats; I predicted that these would undergo local extinction across most of the central Pacific Ocean during regressions, and would expand back into the region during high sea stands. An examination of the fossil record of bivalves on Niue and other central Pacific islands provides support for both of these hypotheses, and shows that the range of some inner-reef specialists can vary substantially among high sea stands. Despite such unstable ranges, limited data do not indicate higher global extinction rates for inner-reef specialists. Sea-level fluctuations can provide vicariant opportunities for speciation, but also impede the potential for geographic differentiation of populations of inner-reef specialist taxa, because the lifespan of insular populations is often limited to the duration of single high sea stands.

To understand the origins of the present distribution and diversity of organisms, one must consider the dynamics of species ranges. Are species ranges relatively stable through time or fluctuating? What factors influence the relative stability of species distributions, and what are the evolutionary consequences of varying degrees of range stability? Climatic cycles caused by orbital variation (Milankovitch cycles) are perhaps the most important agents affecting species distributions, and operate on the time scale between ecological and evolutionary time (Bennett, 1990). Such cycles have resulted in major changes in species distributions and consequently in community composition on land (*e.g.* Davis, 1981; Webb, 1987). In marine habitats climatic cycles are manifested in a variety of ways, including changes in temperature, patterns of ocean circulation, and large-scale fluctuations in sea level. Here I examine how changes in sea level have affected the stability of insular bivalve populations, and consequently the distribution of bivalve species in the central Pacific Ocean. I also consider how range stability can influence extinction and speciation in the area.

Sea-level fluctuations lead to striking changes in shallow-water environments, affecting the extent, nature, and distribution of a variety of habitats. The reef geomorphology of central Pacific islands is such that the effects of sea-level fluctuations are particularly clear. Atolls, as well as fringing and barrier reefs around volcanic islands, can each be categorized into outer- (= fore) and inner-reef components; these components are markedly different in phys-

iography, habitats available, and fate during sea-level fluctuations (Paulay, 1990).

Inner-reef systems, including mangals, reef flats, moats, and lagoons, are separated from the outer reef slope by a shallow, usually intertidal reef margin that often rises at its seawardmost point to form a reef crest. Among islands, inner reefs vary greatly in extent, from narrow, intertidal reef pavements to atoll lagoons hundreds of km² in area. The degree to which they connect with the ocean also varies: from lagoons that are brackish to hypersaline ponds, having no surface connections to the ocean, to those that communicate via wide, deep passages and consequently have oceanic qualities (Salvat, 1967; Chevalier, 1979). Most inner-reef systems are dominated by soft sediments, with grain size ranging from mud to sand to reef rubble, depending primarily on the size of the reef system and its connectivity with the open ocean. Because even the deepest lagoons are shallower than the greatest regression during a glacial cycle (Stoddart, 1973), inner-reef habitats are periodically stranded in their entirety, and exhibit a variety of intermediate stages at other stages of the sea-level cycle (Paulay, 1991). In contrast, outer reef slopes are steep, narrow fringes seaward of inner reefs, show much less variation among islands, and are dominated by hard substrata. Sea-level fluctuations only displace outer reefs up or down slope.

Tectonic processes are important in changing the configuration of reef systems, and are ultimately responsible for the origin of islands and their development from

young volcanoes to atolls and seamounts (Darwin, 1842; Grigg, 1982), however, they operate over much longer timescales than do sea-level fluctuations on mid-plate islands (Paulay and McEdward, 1990). Further, although the impact of tectonic processes on individual islands is marked, their effects are not synchronized among islands. Thus unlike eustatic sea-level fluctuations, tectonic changes do not cause basin-wide changes in habitat.

The marked differences in habitats between outer and inner reefs are reflected in their biota: each environment supports many species that are restricted to it. Among bivalves, about one-third of the central Pacific species appear to be restricted to inner-reef habitats. I would expect such species (= "inner-reef specialists") to undergo local extinction when regressions strand their habitats, while species that occur on outer reefs ("outer-reef inhabitants") persist (Paulay, 1990). If such is the case, inner-reef specialists could have highly dynamic ranges that expand and contract as sea levels rise and fall. Their populations could survive in refugia during low sea stands, re-expanding to the Micronesian and Polynesian islands of the Pacific Plate during each high stand. Likely refugia include islands of the Melanesian arc (New Guinea - Solomons - Vanuatu - Fiji; Fig. 1) and continental islands to the west: these areas have complex reef systems, where inner reef-like habitats persist at all sea stands (Paulay, 1990).

Here I use the fossil record of bivalves on Niue and

other central Pacific islands to test the hypotheses (1) that regressions cause the extinction of inner-reef specialists but not of outer-reef inhabitants, and (2) that inner-reef specialists experience the predicted range contractions and expansions in the central Pacific through successive sea-level cycles. I also look at the long-term consequences of stability versus turnover for insular populations. After reviewing the relevant insular setting and methods, I discuss each of these three points in turn.

INSULAR SETTING

The effects of sea-level fluctuations can be examined on islands that have been uplifted by tectonic forces, and thus have experienced a recent, localized (isostatic) sea-level fall. One can compare the fossil fauna of inner reefs that formed prior to uplift, when the island experienced a localized high-sea stand, with the living fauna surviving on the emergent island at present. Such uplifted limestone islands are uncommon on the largely subsiding Pacific Plate, and include (1) islands raised by lithospheric flexure around new volcanic loads in the Hawaiian, Tuamotu, Pitcairn, Austral, and Cook Island groups; (2) islands apparently raised by lithospheric arching prior to subduction (Niue, Fais); (3) a few islands whose emergence is poorly understood (Banaba, Nauru) (Dubois *et al.*, 1975; McNutt and Menard, 1978; Pirazzoli and Montaggioni, 1985; Spencer *et al.*, 1987). Tectonic uplift is common

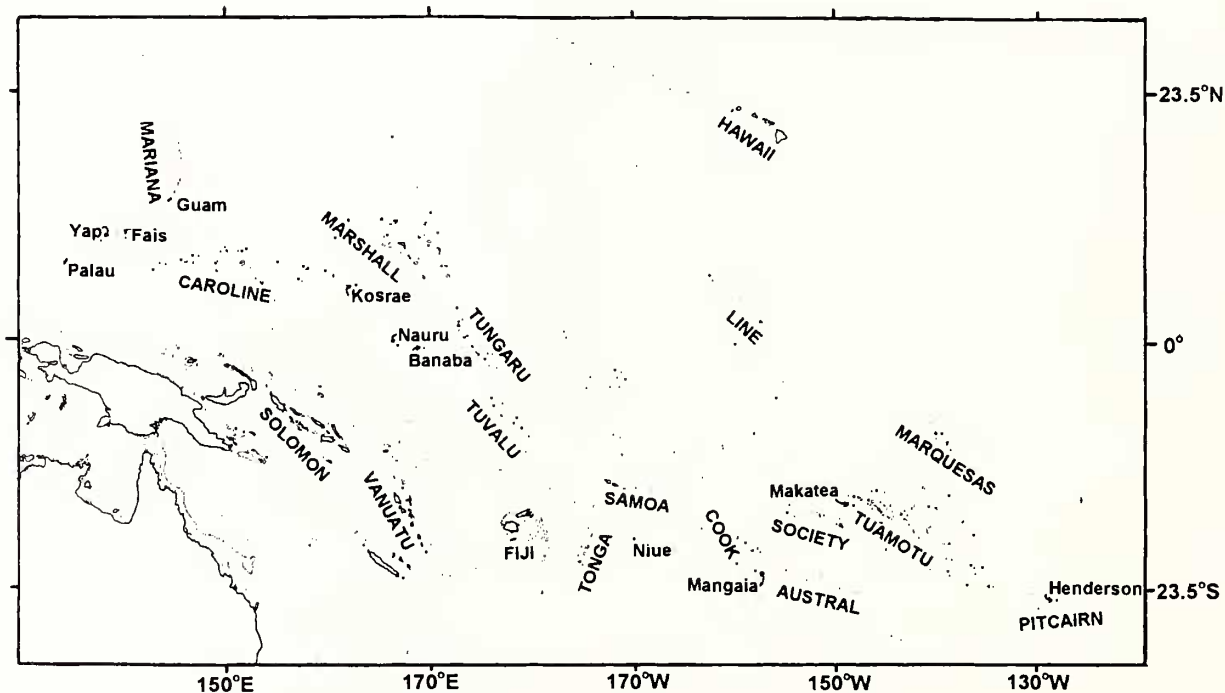


Fig. 1. Map of Pacific islands. Island names in lower case, island group names capitalized.

along the island arcs that line the western plate margin (Mariana - Palau - Melanesian Arc - Tonga), and some of these arc islands (Solomons, Vanuatu) were secondarily accreted onto the Pacific Plate.

Six limestone islands that formed on the Pacific Plate lack exposed volcanics and could be uplifted atolls: Nauru, Banaba, Fais, Makatea, Niue, and Henderson. The first three are poorly known, and together with Makatea have been mined for phosphate - an activity which disturbs paleolagoonal deposits considerably. Makatea has received more attention than the first three. However the atoll, apparently Miocene in age, has suffered from considerable diagenesis as well as mining (Montaggioni, 1985). Both Niue and Henderson sustain well-preserved lagoonal deposits with rich fossil communities dating from the Pliocene and Pleistocene respectively (Paulay and Spencer, 1988, 1992; Spencer and Paulay, 1989).

Niue lies 400 km east of the Tongan island arc (Fig. 1). The island's uplift is thought to be the result of arching of the Pacific Plate prior to its subduction into the Tongan Trench (Dubois *et al.*, 1975). The core of Niue comprises an uplifted atoll with the original atoll form well preserved: a ring of reef limestones reaching an elevation of 68 m encircles a lagoonal depression (34 m) of calcarenites (Schofield, 1959; Paulay and Spencer, 1992). Surface deposits in the lagoon are of late Pliocene age [(1.7)-2.0-2.2 Ma; dates based on Sr isotope ratios, P. Aharon, pers. comm., 1995]. While the peripheral core atoll reef facies has undergone considerable diagenesis and has generally poor fossil preservation, the molluscan fauna of the central lagoon is well-preserved at many locations. Several marginal, Pleistocene apron reefs have been accreted onto the atoll core since initiation of uplift, some forming parts of the terraces that surround the island. These younger reefs have additional, often very well-preserved, molluscan assemblages.

Since uplift, a limited inner reef has developed around Niue: a narrow reef platform especially pronounced on the leeward half of the coastline. The reef platform is an intertidal to shallow subtidal (< 0.5 m, except for a few deeper pools) reef pavement with pockets of coarse sediments, fronted by a well-developed intertidal reef crest. Eight species of inner-reef-specialist bivalves [*e. g. Fragum mundum* (Reeve, 1845), *Isognomon perna* (Linné, 1767), *Isognomon cf. laticostata* (Reeve, 1858)] occupy this habitat (Paulay, 1990 and unpub.). Much of the windward coast has no inner-reef development, or has only narrow (< 10 m), elevated (> 1 m above high-water level) splash pools.

The outer reef slope around Niue generally begins as a steep incline, meeting a gently sloping, sandy terrace (ca. 50-100 m wide) at 25-50 m depth. In some embayments (at Alofi and Avatele), limited submarine terracing occurs also at shallower depths. Despite these terraces, the

100 m isobath lies within 200-400 m of the reef crest (Schofield, 1959). As on most central Pacific islands, the outer reef slope is dominated by hard substrata, with mobile sediments limited to sand pockets (often substantial) in reef grooves, and to the sand- and rubble-dominated terrace at 25-50 m depth.

MATERIALS AND METHODS

In 1986 and 1991, I collected fossils at 19 sites in the fossil atoll lagoon and 21 sites in the surrounding core and apron reef facies, selecting sites for their accessibility and fossil preservation. Most of the lagoonal sites were at calcarenite quarries: bulldozed pits used in supplying sand for construction. Active and abandoned quarries of unconsolidated calcarenites are scattered throughout Niue's interior, many of them noted on the Map of Niue (NZMS, 1985). The vertical extent of quarries varies from ca. 1 to 8 m, with most in the 1-3 m range; their horizontal extent ranges from a few tens to hundreds of meters. A few quarries show striking vertical changes in fossil assemblages and diagenesis; this, together with aspects of intersite faunal variation (Paulay, unpub.) and a spread in Sr isotope dates (Wheeler and Aharon, 1991; Aharon *et al.*, 1993; P. Aharon, pers. comm., 1995), indicates that lagoonal faunas exposed in quarries likely date from more than one high sea stand. Most of the sediments now found on the lagoon surface were apparently deposited over only a few high sea stands during the late Pliocene, judging from general faunal similarity, limited vertical spread (< 25 m across the entire lagoon), and relatively narrow range of Sr dates [(1.7)-2.0-2.2 Ma; P. Aharon, pers. comm., 1995].

I sampled the recent fauna by SCUBA on the outer reef slope and by snorkeling and reef walking on the reef flat. Results of the 1986 survey are listed in Paulay (1990); the 1991 survey added several new records. The single bivalve species [*Fragum fragum* (Linné, 1758)] recorded from Niue by Cernohorsky (1970; and relisted in Paulay, 1990) is here removed from the faunal list: in my extensive surveys, I did not find *F. fragum*, appropriate habitat for which is absent on the island. The similar *F. mundum* inhabits reef flats on Niue. As previously noted (Paulay, 1987), several of Cernohorsky's bivalve identifications (including *Fragum* identifications) in a similar list published on the fauna of the neighboring Cook Islands have proved to be incorrect.

I used the extensive Indo-West Pacific collections and library resources of the U. S. National Museum of Natural History (USNM) to aid in taxonomic work. T. R. Waller (USNM) kindly identified the pectinid species. I identified fossil specimens that matched living species as such, and labeled those that were close to living forms but differed slightly but consistently from the range of variation

exhibited by Recent specimens with "cf." I noted those fossils that differed markedly enough from living species to be considered specifically distinct with "aff." Several of the latter could be ancestral to Recent species. Specimens that were not sufficiently well-preserved for a definitive identification but otherwise matched a Recent species were labeled with "?". Fossils belonging to fairly well-known groups that did not match or approximate any living forms encountered in collections or the literature, I assumed to be globally extinct. The global survival (extinct or extant) of species that belong to poorly known taxa (mostly micro-lucinids) was left unresolved. I listed species too poorly preserved for specific identification under the lowest category to which they were identified and without numerical species designation. Although I listed the taxonomically poorly known and poorly preserved species (Table 1), these were not included in the analyses below. A taxonomic review of the fossil fauna will be presented elsewhere.

RESULTS AND DISCUSSION

TURNOVER AND STABILITY ON NIUE

I recognize 104 species of fossil bivalves on Niue: 83 from the fossil lagoon, nine from probable atoll-core fore-reef facies encircling the lagoon, and 30 from marginal mid-late Pleistocene reefs (Table 1). The stratigraphic demarcation between Pliocene atoll-core fore-reef facies and marginal, older Pleistocene apron reefs (which could have been secondarily accreted onto the core after initiation of uplift) is poorly understood. Unless otherwise noted, all discussion below concerns the Pliocene lagoonal fauna. Twelve of the 83 lagoonal species are either very poorly preserved, or belong to taxonomically poorly known groups, and will not be further considered unless otherwise noted (Table 1).

Among the remaining 71 lagoonal species, 20 (28%) appear to be globally extinct. Six of the 20 (*Excellichlamys* aff. *spectabilis*, *Laevichlamys* aff. *squamosa*, *Tellina* aff. *crucigera*, *Wallucina* aff. *haddoni*, *Pillucina* aff. *spaldingi*, and *Corculum* aff. *cardissa*) are close, and might be ancestral, to the Recent species named; thus their disappearance could represent pseudoextinction. Considering the possibility of pseudoextinction, the rate of global extinction for the fauna is 20-28%. This is comparable to the level of extinction experienced by Japanese and Californian bivalves of the same age, and is similar to background levels of extinction for the class (Stanley *et al.*, 1980). There is thus no evidence for any major extinction events affecting the fauna since the late Pliocene. In addition to the six species noted above, two additional ones (*Fragum* cf. *fragum*, *Timoclea* cf. *marica*) show limited morphological disparity from Recent populations. Thus

despite their characteristically slow rate of evolution (Simpson, 1953; Stanley, 1979), up to 14% (N = 57) of the surviving bivalve species in the fauna could have undergone morphological change since the latest Pliocene.

Local extinction among the 51 extant lagoonal species was 62%. Is this high extinction rate due to changes in habitat or to a general instability of species distributions on isolated oceanic islands? Data on taxonomic affinity, microhabitat use, and zonation indicate that regression-caused habitat change was the predominant cause of local extinction.

The Pliocene and Recent habitats compared are quite different: the Pliocene's shallow lagoon, dominated by reef sands versus today's narrow reef flats and steep outer reef slope, dominated by hard substrata. This difference is reflected in the taxonomic composition of the fauna (Fig. 2, Table 2): taxa that prefer outer reef habitats (*e. g.* pectinoids) are proportionately better represented in the Recent fauna, while groups that prefer lagoonal soft bottoms (*e. g.* tellinoids) (Paulay, 1990) are better represented in the Pliocene fauna. Both the Pliocene and Recent faunas are composed solely of pteriomorph and heterodont (defined as in Boss, 1982, but not Waller, 1990, to include the few myoids) bivalves, as is typical of the shallow-water fauna of all central Pacific islands. The ratio of pteriomorphs to heterodonts is lower in the Pliocene lagoonal fauna than among species living on Niue today (0.57 versus 0.93), albeit not significantly so (G-test, $G = 2.52$, $p > 0.05$). The lower proportion of pteriomorphs in the Pliocene runs counter to a taphonomic bias favoring the preservation of the frequently calcitic shells of pteriomorphs over the almost strictly aragonitic shells of heterodonts. The difference between Pliocene and Recent pteriomorph / heterodont ratios could reflect differences in microhabitat use: while the majority of pteriomorphs prefer hard substrata, the majority of heterodonts live in soft sediments. Thus in South Polynesia, 92% of pteriomorphs and 23% of heterodonts live on or in hard substrata (data from Paulay, 1990: appendix). Indeed, soft-bottom species are better represented (G-test, $G = 5.75$, $p < 0.05$) in the Pliocene than in the Recent fauna of Niue (Fig. 3). An analogous trend is found in the Recent fauna of South Polynesia: a significantly greater proportion of inner-reef specialists occur among soft-bottom than among hard-bottom species (Paulay, 1990).

On Niue, the contrasting fates of inner-reef specialists and outer-reef inhabitants support the hypothesis that the major cause of local extinction for the Pliocene fauna was uplift-associated habitat loss. The habitat specificities of all but four of the 51 extant species are known to some degree (Table 1). Inner-reef specialists suffered complete (100%, N = 20) local extinction with uplift; the limited inner-reef specialist assemblage inhabiting the reef flats of

Table 1. Fossil bivalves from Niue. ID (quality of identifications): +/+, species sufficiently well preserved to be identifiable and identified; +/-, species sufficiently well preserved to be identifiable but taxonomic problems with identification at present; -/-, species not sufficiently well preserved to be identifiable to species. Core Lagoon: found (1) or not found (0) in lagoonal facies in island interior. Core? Fore reef: found (1) or not found (0) in fore-reef facies judged to represent original core reef of island. Marginal Fore reef: found (1) or not found (0) in marginal, Pleistocene apron reefs secondarily accreted onto island since initiation of uplift. Globally extant?: globally extant (1), globally extinct (0). Locally extant?: locally extant (1), locally extinct (0). Range to W: known (1) or not known (0) from islands to west of Niue. Range to E: known (1) or not known (0) from southeastern Polynesia. Habitat: I, inner reefs only; O, outer reefs only; IO, inner and outer reefs.

Family	Species	ID	Core	Core?	Marginal	Globally	Locally	Range	Range	Habitat
			Lagoon	Fore reef	Fore reef	Extant?	Extant?	to W	to E	
Arcidae	<i>Arca avellana</i> Lamarck, 1819	+/+	1	0	1	1	1	1	1	IO
	<i>A. ventricosa</i> Lamarck, 1819	+/+	1	0	0	1	0	1	1	I
	<i>A. plicata</i> (Dillwyn, 1817)	+/+	0	0	1	1	1	1	1	O
	<i>A. sp. 1</i>	+/+	1	0	0	0?	0	?	?	?
	<i>Barbatia amygdalumtostum</i> (Röding, 1798)	+/+	0	1?	1	1	0	1	0	IO
	<i>B. foliata</i> (Forsskål, 1775)	+/+	1	0	0	1	0	1	1	I
	<i>B. ?parva</i> (Sowerby, 1844)	+/+	1	0	0	1	1	1	1	IO
	<i>B. ?setigera</i> (Reeve, 1944)	+/+	1	0	0	1	0	1	1	IO
	<i>B. sp. 1</i>	+/+	0	0	1	1	1	1	0	IO
	<i>B. sp. 8</i>	+/+	1	0	0	0	0	?	?	?
	<i>Hawaiarca rectangula</i> (Dall, Bartsch and Rehder, 1938)	+/+	0	0	1	1	1	0	0	IO
	<i>Anadara ?uropigimelana</i> (Bory de St. Vincent, 1824)	+/+	1	0	0	1	0	1	1	I
	Noetiidae	<i>Arcopsis ornata</i> (Viader, 1951)	+/+	1	0	0	1	0	1	0
Glycymerididae	<i>Glycymeris laddi</i> (Abrard, 1946)	+/+	1	0	0	0	0	1	?	?
	<i>Tucetona fijiensis</i> (Ladd, 1934)	+/+	0	1	0	0	0	1	?	?
Philobryidae	<i>Cratis ?kanekoi</i> Hayami and Kase, 1993	+/+	1	0	0	1	1	1	0	IO
Mytilidae	<i>Botula fusca</i> (Gmelin, 1791)	+/+	1	0	0	1	0	1	1	IO
	<i>Lithophaga</i> sp(p).	-/-	1	1	0	?	?	?	?	?
	<i>?Fungiacava</i> sp.	-/-	0	0	1	?	?	?	?	?
	<i>Modiolus ?auriculatus</i> Krauss, 1848	+/+	0	0	1	1	1	1	1	I
	<i>?Septifer</i> sp.	-/-	1	0	0	?	?	?	?	?
	<i>?Mytilidae</i> n. gen. sp. 1	+/+	1	0	0	0	0	?	?	?
Pinnidae	<i>Pinnidae</i> sp.	-/-	1	0	0	?	?	?	?	?
Ostreidae	<i>Ostreidae</i> sp. 1	+/+	1	0	0	1	0	1	0	I
Anomiidae	<i>Anomia</i> sp.	+/-	1	0	0	?	?	?	?	?
Pteriidae	<i>Pinctada</i> sp.	-/-	1	0	0	?	?	?	?	?
Isognomonidae	<i>Isognomon</i> sp.	+/-	0	0	1	?	?	?	?	?
Limidae	<i>Lima vulgaris</i> (Link, 1807)	+/+	1?	1	1	1	0	1	1	IO
	<i>Limaria ?fragilis</i> (Gmelin, 1791)	+/+	1	0	0	1	1	1	1	IO
	<i>Ctenoides annulatus</i> (Lamarck, 1819)	+/+	1	0	0	1	1	1	0	IO
Plicatulidae	<i>Plicatula</i> sp(p).	+/-	1	0	1	?	?	?	?	?
Pectinidae	<i>Gloripallium</i> sp. 1	+/+	1	0	0	0	0	?	?	?
	<i>G. pallium</i> (Linné, 1758)	+/+	1	0	1	1	1	1	1	IO
	<i>Laevichlamys irregularis</i> (Sowerby, 1842)	+/+	1	0	0	1	1	1	1	IO
	<i>L. aff. squamosa</i> (Gmelin, 1791)	+/+	1	0	0	0	0	?	?	?
	<i>Semipallium tigris</i> (Lamarck, 1819)	+/+	1	0	1	1	1	1	1	IO
	<i>S. amicum</i> (Smith, 1885)	+/+	0	0	1	1	1	1	0	O
	<i>Excellichlamys aff. spectabilis</i> (Reeve, 1853)	+/+	1	0	0	0	0	?	?	?
	<i>Mirapecten rastellum</i> (Lamarck, 1819)	+/+	0	0	1	1	1	1	1	O
	Spondylidae	<i>Spondylus violacescens</i> Lamarck, 1819	+/+	0	0	1	1	1	1	1
	<i>S. sp(p).</i>	+/-	1	1	1	?	?	?	?	?
Lucinidae	<i>Codakia punctata</i> (Linné, 1758)	+/+	1	0	0	1	1	1	1	IO
	<i>C. tigerina</i> (Linne, 1758)	+/+	1	0	0	1	1	1	1	IO
	<i>"Ctena" bella</i> (Conrad, 1837)	+/+	1	0	1	1	1	1	1	IO
	<i>Wallucina aff. haddoni</i> (Melvill and Standen, 1899)	+/+	1	0	0	0	0	?	?	?
	<i>W. sp. 4</i>	+/-	1	0	0	?	0	?	?	?
	<i>Pillucina aff. spaldingi</i> (Pilsbry, 1921)	+/+	1	0	0	0	0	?	?	?
	<i>Anodontia edentula</i> (Linné, 1758)	+/+	1	0	1	1	1	1	1	IO
	<i>"Parvilucina" sp. 1</i>	+/-	1	0	0	?	0	?	?	?
	<i>"P." sp. 2</i>	+/-	1	0	0	?	0	?	?	?
	<i>Bellucina</i> sp. 1	+/-	1	0	0	?	0	?	?	?

(continued)

Table 1. (continued)

Family	Species	ID	Core	Core?	Marginal	Globally	Locally	Range	Range	Habitat
			Lagoon	Fore reef	Fore reef	Extant?	Extant?	to W	to E	
Fimbridae	<i>Fimbria</i> sp. 1	++	1	0	0	0	0	?	?	?
	<i>F.</i> sp. 2	++	0	1	0	0	0	?	?	?
Chamidae	<i>Chama lazarus</i> Linné, 1758	++	1	0	0	1	0	1	0	I
	<i>C. asperella</i> Lamarck, 1819	++	1	0	1	1	1	1	1	IO
	<i>C. iostoma</i> Conrad, 1837	++	0	0	1	1	1	1	1	IO
	<i>C.</i> sp. 4	++	0	0	1	1	1	1	0	O
	<i>C.</i> sp. 7	++	1	0	0	0?	0	?	?	?
	<i>Cardita variegata</i> Bruguière, 1792	++	1	0	0	1	0	1	1	I?
Cardiidae	<i>Vasticardium</i> n. sp. (Vidal, pers. comm.)	++	1	0	0	1	0	1	0	?
	<i>V. orbita philippinense</i> (Hedley, 1899)	++	1	0	1	1	1	1	0	IO
Tellinidae	<i>Acrosterigma</i> sp. 1	++	1	0	0	0	0	?	?	?
	<i>Ctenocardia</i> aff. <i>fornicata</i> (Sowerby, 1841)	++	0	1	0	0	0	?	?	?
	<i>Microfragum</i> ? <i>festivum</i> (Deshayes, 1855)	++	0	0	1	1	1	1	0	O
	<i>Fragum</i> sp. 1	++	1	0	0	0	0	?	?	?
	<i>F.</i> cf. <i>fragum</i> (Linné, 1758)	++	1	0	0	1	0	1	1	I
	<i>Corculum</i> sp. 1	++	1	0	0	0	0	?	?	?
	<i>C.</i> aff. <i>cardissa</i> (Linné, 1758)	++	1	0	0	0	0	?	?	?
	<i>Hippopus hippopus</i> (Linné, 1758)	++	1	0	0	1	0	1	0	I
	<i>Tridacna maxima</i> (Röding, 1798)	++	1	0	1	1	1	1	1	IO
	<i>T. squamosa</i> Lamarck, 1819	++	0	0	1	1	1	1	1	IO
	<i>T. derasa</i> (Röding, 1798)	++	1	0	0	1	0	1	0	I?
	<i>T. gigas</i> (Linné, 1758)	++	1	0	0	1	0	1	0	I?
	<i>Tellina</i> aff. <i>crucigera</i> Lamarck, 1818	++	1	0	0	0	0	?	?	?
	<i>T. chariessa</i> Salisbury, 1934	++	1	0	0	1	0	1	0	I?
	<i>T. remies</i> Linné, 1758	++	1	0	0	1	0	1	0	I?
<i>T. scobinata</i> Linné, 1758	++	1	0	0	1	1	1	1	IO	
<i>T. gargadia</i> auctt. non Linné, 1758	++	1	0	0	1	0	1	0	I?	
<i>T. bougei</i> Sowerby, 1909	++	1	0	0	1	1	1	1	IO	
<i>T. robusta</i> Hanley, 1844	++	1	0	0	1	0	1	1	I	
<i>T.</i> sp. 1	++	1	0	0	0	0	?	?	?	
<i>T. (Pinguitellina)</i> sp. 1	++	1	0	0	0	0	?	?	?	
<i>T. semen</i> Hanley, 1845	++	1	0	0	1	0	1	1	IO	
<i>Loxoglypta clathrata</i> (Deshayes, 1835)	++	1	0	0	1	1	1	1	IO	
<i>Scissulina dispar</i> (Conrad, 1837)	++	1	0	0	1	0	1	1	I	
<i>Macominae</i> sp. 1	+/-	1	0	0	?	0	?	?	?	
Semelidae	<i>Semelangulus crebrimaculatus</i> (Sowerby, 1868)	++	1	0	1	1	1	1	1	IO
	<i>S.</i> sp. 3	++	0	0	1	1	1	1	0	IO
	<i>Leptomya psittacus</i> Hanley, 1882	++	1	0	0	1	0	1	0	I
Psammobiidae	<i>Ervilia bisculpta</i> Gould, 1861	++	1	0	0	1	0	1	1	IO
	<i>Gari squamosa</i> (Lamarck, 1818)	++	1	0	0	1	0	1	0	?
Mesodesmatidae	<i>G. pusilla</i> Bertin, 1880	++	1	0	0	1	0	1	0	?
	<i>Atactodea striata</i> (Gmelin, 1791)	++	1	0	0	1	0	1	0	I?
Trapezidae	<i>Coralliophaga coralliophaga</i> (Gmelin, 1791)	++	1	0	0	1	0	1	1	?
	<i>Trapezium oblongum</i> (Linné, 1758)	++	1	0	1	1	1	1	1	IO
	<i>Glossocardia</i> ? <i>stoliczkana</i> Prashad, 1932	++	0	1	0	1	0	1	0	?
Veneridae	<i>G. obesa</i> (Reeve, 1843)	++	1	0	0	1	0	1	1	I
	<i>Globivenus toreuma</i> (Gould, 1850)	++	0	1	1	1	1	1	1	IO
	<i>Periglypta reticulata</i> (Linné, 1758)	++	0	0	1	1	1	1	1	IO
	<i>Lioconcha ornata</i> (Dillwyn, 1817)	++	1	0	0	1	1	1	1	IO
	<i>Pitar</i> sp. 7	++	1	0	0	0	0	?	?	?
	<i>Timoclea</i> cf. <i>marica</i> (Linné, 1758)	++	1	0	0	1	0	1	0	I
	<i>Gafrarium pectinatum</i> (Linné, 1758)	++	1	0	0	1	0	1	1	I
<i>G.</i> sp. 1	++	1	0	0	0	0	?	?	?	

Niue today includes none of the species of the Pliocene lagoon (Fig. 4). Most (77%) of the locally extinct species in the Pliocene lagoon fauna are inner-reef specialists.

In contrast, among outer-reef inhabitants, only 22% (six of 27 species) suffered local extinction (Fig. 4). Further, three (*Tellina semen*, *Arcopsis ornata*, *Ervilia bisculpta*) of the six species not found living on Niue are micromollusks, which I sampled less thoroughly in the Recent than in the Pliocene biota. Thus, the data indicate that the ranges of species whose habitat is not drastically altered by sea-level fluctuations exhibit long-term stability.

Similar distributional stability is exhibited by the fauna of the Pleistocene fore reefs deposited onto the atoll core around the periphery of Niue. These marginal reef deposits formed after initiation of island uplift, and represent habitats comparable to those on today's outer reef. Thus, no major change in available habitats occurred between the time of these Pleistocene faunas and today, a time spanning at least one full sea-level cycle. Only two (8%, N = 26) of the identified bivalves encountered in these peripheral deposits were not encountered in the Recent fauna: *Lima vulgaris* and *Barbatia amygdalumtostum*. The former species is ubiquitous in southern Polynesia today, but was not found living on Niue. The latter species today ranges no further east than Tonga and Samoa, however, the fossils indicate that during at least a brief period in the Pleistocene, *B. amygdalumtostum* extended as far east as Niue. Among Recent bivalve species on Niue, two appear to be restricted to western Pacific islands today; these two occur in Niue's Pleistocene reef deposits, indicating some long-term stability to their ranges. One of the two, *Sempallium amicum*, is common today on Niue and is fur-

Table 2. Comparison of per-family species richness between Pliocene lagoonal fauna and Recent fauna of Niue Island. Number of species given for each family under each fauna.

Family	Pliocene	Recent
Arcidae	8	6
Noetiidae	1	0
Glycymerididae	1	0
Philobryidae	1	1
Mytilidae	4	4
Pinnidae	1	2
Ostreidae	1	0
Gryphaeidae	0	1
Anomiidae	1	1
Dimyidae	0	1
Pteriidae	1	2
Isognomonidae	0	2
Malleidae	0	1
Limidae	3	5
Plicatulidae	1	1
Propeamussiidae	0	1
Pectinidae	6	9
Spondylidae	1	4
Lucinidae	10	6
Fimbriidae	1	0
Chamidae	3	7
Carditidae	1	0
Cardiidae	11	8
Tellinidae	13	6
Semelidae	3	6
Psammobiidae	2	2
Mesodesmatidae	1	0
Trapezidae	3	1
Glossidae	0	1
Veneridae	5	5
Corbulidae	0	1
Gastrochaenidae	0	1

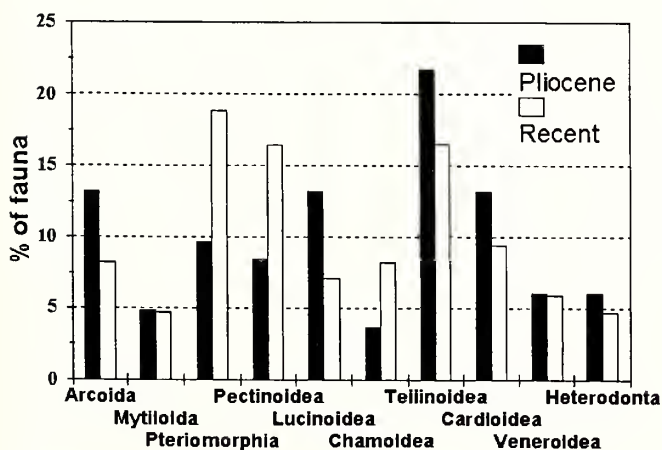


Fig. 2. Comparison of diversity of suprafamilial taxa between Pliocene lagoonal fauna (N = 83 species) and Recent fauna (N = 85 species) of Niue. Pteriomorphia = other than Arcoida, Mytiloidea, and Pectinoidea; Heterodonta = other than Lucinoidea, Chamoidea, Tellinoidea, Cardioidea, and Veneroidea, includes two myoids in Recent fauna.

ther known from Palau and Tonga (T. R. Waller, pers. comm.). The other species, *Barbatia* sp. 1 (apparently undescribed), is presently abundant on Niue, and also occurs on eastern Fiji, Wallis Island, and Palmerston Atoll.

GEOGRAPHIC RANGE CONTRACTIONS

A corollary to the observation that inner-reef specialists undergo extinction in the central Pacific during regressions is that lagoonal faunas in the area are reassembled anew during each high sea stand. Given the limited time available during each high sea stand and the somewhat stochastic nature of dispersal, the geographic ranges of species might be different at different high sea stands. There is evidence for such range differences in Niue's fossil fauna (Paulay, unpub.), as well as in the fossil record of central Pacific bivalves. With regard to the latter, in surveys of the fossil bivalve faunas of Polynesian and Micronesian islands, I have encountered four species that are each known as fossils on two or more islands on which they are not extant. The fact that these range contractions involve more than one island supports the hypothesis that

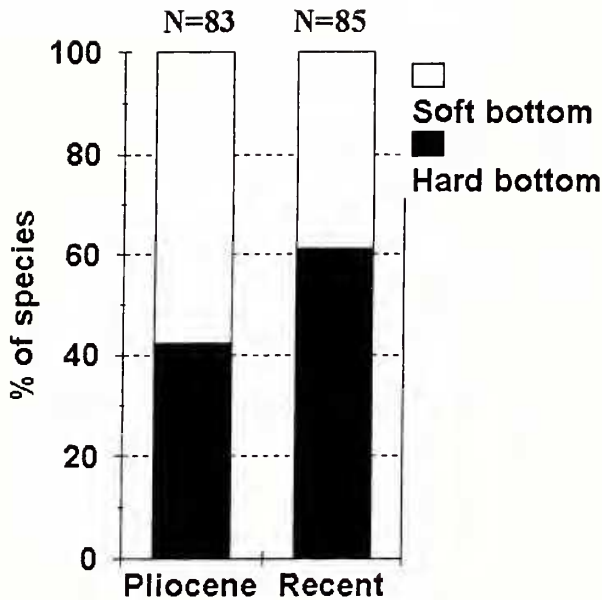


Fig. 3. Comparison of proportions of soft-bottom versus hard-bottom species between Pliocene lagoonal fauna and Recent fauna of Niue. Proportions significantly different between the two faunas (G-test, $p < 0.05$).

regional rather than local processes were responsible for the local extinctions. All four species - *Septifer excisus* (Wiegmann, 1837), *Anadara antiquata* (Linné, 1758), *Tridacna gigas*, and *Hippopus hippopus* - are largely or entirely restricted to inner reefs, as discussed below.

The mussel *Septifer excisus* forms large aggregations on intertidal reef flats in the Mariana Islands, although occasional individuals are also found in cryptic habitats on the fore reef. Its present range extends from East Africa and the Red Sea to the Philippine and Mariana Islands (Fig. 5). While the species does not appear to reach the Pacific Plate today, it reached the most isolated islands of the Pacific Plate during the Pleistocene. It was common in the Hawaiian Islands in shallow water Pleistocene communities (Kosuge, 1969; as *Septifer vaughani* Dall, Bartsch and Rehder, 1938, a synonym, Paulay, 1996), was locally abundant in the shallowest late Pleistocene apron reefs of Mangaia (Cook Island), and was occasional in the Pleistocene lagoon of Henderson Island (Pitcairn Group) (Paulay, 1996).

Anadara antiquata and *A. uropigimelana* are two species in the genus that inhabit islands of the Pacific Plate; both appear to be inner-reef specialists (Paulay, 1990 - both listed as *A. antiquata*). *A. antiquata* extends from East Africa and the Red Sea (Kilburn, 1983) to at least the Mariana Islands and Fiji, with fossil specimens known from the Hawaiian Islands (Kay, 1979) and Aitutaki (Cook Island; Paulay, unpub.). *A. uropigimelana* extends from

East Africa (Kilburn, 1983) to the Society Islands and shows local extinction on Niue.

The giant clams *Tridacna gigas* and *Hippopus hippopus* are also largely restricted to inner reefs. *T. gigas* can be common in shallow lagoonal areas, but is very rare on the steep slopes of outer reefs. The species is presently restricted to the western Pacific (Fig. 6). Its range contracted slightly during the Holocene due to apparently human-caused extirpations in the Carolines (Yap: Price and Fagolimul, 1988; Kosrae: pers. obs.) and Fiji (Lewis *et al.*, 1988). However, *T. gigas* suffered range contraction even prior to the arrival of humans: Plio-Pleistocene but no Holocene fossils are known from Guam (Rosewater, 1965; H. G. Siegrist, pers. comm.), Aldabra (Taylor, 1978), Kenya (Crame, 1986), and Niue.

Hippopus hippopus is the giant clam most limited in its depth tolerance: it is restricted to very shallow (< 3 m) reef flats and moats, and is absent from outer reef slopes (R. Rowan, pers. comm.). Its shallow zonation makes this species especially vulnerable to human predation as well as to sea-level fluctuations, both of which appear to have contributed to limiting the present distribution of the species. Today, *H. hippopus* is confined to the western Pacific from western Indonesia to the Marshall Islands and Tonga (Fig. 7). The occurrence of Holocene subfossils but absence of living animals on Guam (B. D. Smith, pers. comm.; pers. obs.) and Fiji (Lewis *et al.*, 1988), and the possible recent

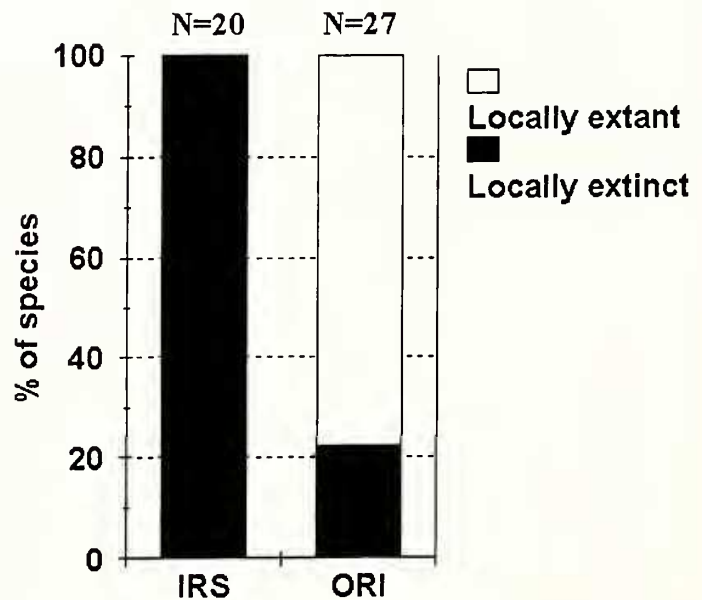


Fig. 4. Comparison of frequency of local extinction among inner-reef specialist (IRS) species versus among outer-reef inhabitant (ORI) species. Proportions significantly different between the two groups (G-test, $p < 0.001$). Only globally extant, Pliocene lagoonal species with known habitat specificity are considered.

extinction in Tonga (Lewis *et al.*, 1988), likely reflect human predation. However, the species also experienced pre-Holocene range contractions at both its eastern (Niue) and western (Aldabra: Taylor, 1978) distributional boundary, probably due to sea-level fluctuations.

The above distributional changes of inner-reef bivalve species supports the hypothesis that the ranges of inner-reef specialists in the central Pacific differ between different high sea stands. The significant range contractions noted in several species since the Plio-Pleistocene demonstrate that at least some of the endemic diversity of the western Pacific is the result of the area being a sink for species that have been extirpated elsewhere. Springer (1982) argued that most taxa that presently do not extend onto the Pacific Plate were always so delimited. Niuean fossils and the species noted above include at least four species that are known as fossils on the Pacific Plate but no longer occur there: *Septifer excisus* (above), *Tridacna derasa* (with an eastern distributional limit along the western Pacific island arcs), *Glossocardia ? stoliczkana* (known extant from Indonesia and the Philippines only; A. Matsukuma, pers. comm.), and *Vasticardium* n. sp. (known from Moluccas, Papua New Guinea, Admiralty Islands, and Solomons only; J. Vidal, pers. comm.).

LONG TERM CONSEQUENCES

The range contractions and expansions discussed here occur in association with Milankovitch cycles. These cycles have a periodicity (20-100 Ma) that lies between ecological timescales, during which typical population

processes operate, and geological timescales, over which much of macroevolutionary change occurs (Bennett, 1990). What are the long-term effects of the recurrent regional extinctions and resulting range contractions suffered by inner-reef specialists? There are a number of hypothesized consequences: (1) a higher global extinction rate among inner-reef specialists than among outer-reef inhabitants, whose metapopulations exhibit relative long-term stability; (2) facilitation of speciation among inner-reef specialists, as regression-caused extinction of intermediate populations divides previously contiguous species ranges (*e.g.* Fleming, 1986; Springer and Williams, 1990); and conversely, (3) inhibition of speciation among inner-reef specialists, as regression-caused extinction on isolated islands precludes the divergence of such populations into island endemics.

The limited evidence available on Niue does not support the hypothesis of higher rates of global extinction among inner-reef specialists than among outer-reef inhabitants. A limitation in testing this hypothesis, however, is that the habitat specificities (with regard to inner versus outer reef) of extinct species cannot be reliably determined. To partially circumvent this problem, I can use one of two alternative proxies - recognizing, however, that these substitute comparisons could fail to detect existing differences in extinction rates. One such proxy compares extinction rates between lagoonal and fore-reef assemblages: lagoonal assemblages have a large proportion (43% among extant species of the Pliocene fauna) of inner-reef specialists, while fore-reef assemblages lack inner-reef specialists

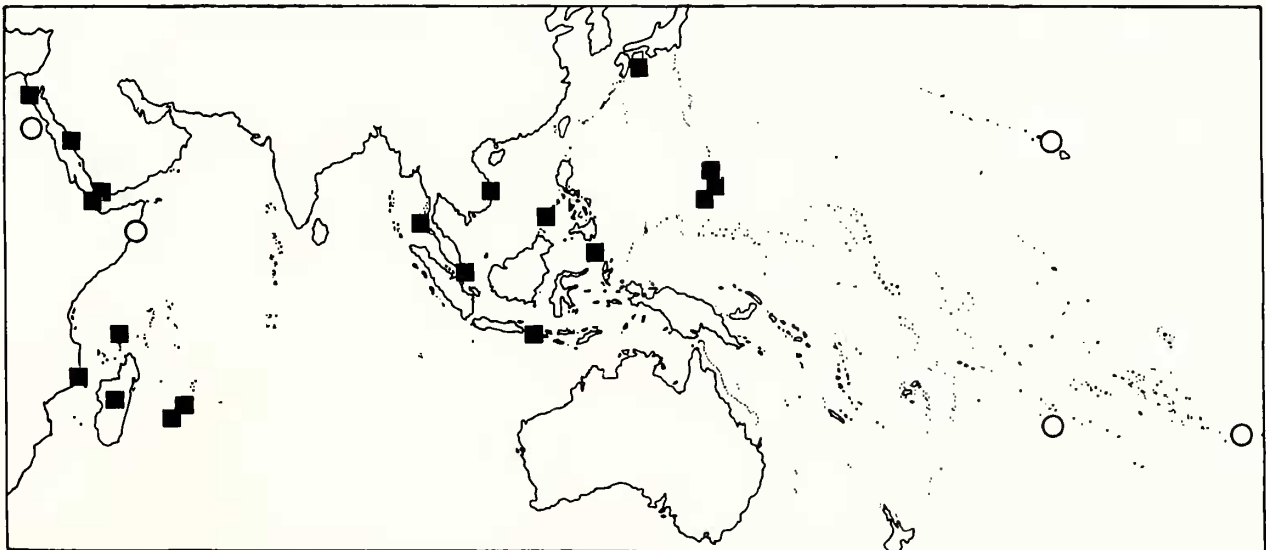


Fig. 5. Present and past distribution of *Septifer excisus*. Based on USNM and Museum of Comparative Zoology records (see Paulay, 1996), and literature records from: Newton (1900), Dautzenberg (1929), Prashad (1932), Lamy (1937), and Abrard (1940). (Squares, extant records; empty circles, Pleistocene records).

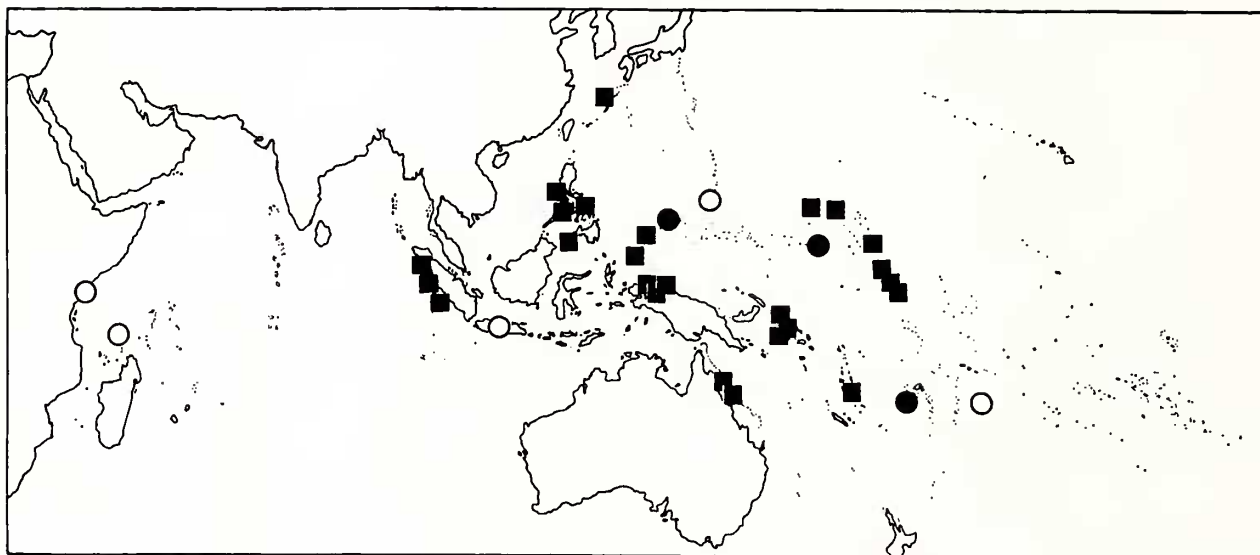


Fig. 6. Present and past distribution of *Tridacna gigas*. Based on literature records from Rosewater (1965), Taylor (1978), Hirschberger (1980), Crame (1986), Lewis *et al.* (1988), Price and Fagolimus (1988), and additional data herein, including additional Marshall and Tungaru records, and Kosrae Holocene record. [Squares, extant records; solid circles, Holocene records, but presumed extinct; empty circles, Plio-Pleistocene records (and Miocene from Java)].

(transport of dead shells from lagoons to fore reefs appears to be negligible on central Pacific islands; Paulay, 1990). Seven identified species are known from putative core fore-reef deposits on Niue (Table 1; see above), and 43% of these are extinct. Among species in the lagoonal assemblage, 28% have gone extinct. These extinction rates are in the opposite direction than predicted.

An alternative proxy compares the proportion of species that were *likely* inner-reef specialists among the extinct portion of the Pliocene fauna with the proportion *known* to be inner-reef specialists among the extant portion of the Pliocene fauna. Three of the extinct species are known from fore-reef deposits and are thus definitely outer-reef inhabitants. Four others belong to genera (*Gafrarium*, *Fragum*, *Corculum*) whose extant species in the Central Pacific are all inner-reef specialists; thus their extinct counterparts were likely also inner-reef specialists. Based on these seven extinct species, the Pliocene fauna (here including both fore-reef and lagoonal deposits) included comparable proportions of inner-reef specialists among its extinct (57%) and extant (43%, N = 47) species.

Sea level fluctuations can be important agents of vicariance, separating once-continuous species ranges by (1) forming terrestrial or oceanographic barriers (*e.g.* Fleminger, 1986) or (2) causing the extinction of intermediate populations (*e.g.* Springer and Williams, 1990). The first of these processes is possibly exemplified in two areas of the Indo-West Pacific (Rosen, 1984): during maximal glacial low-sea stands, emergent land isolated the Red Sea from the western Indian Ocean, and greatly constricted the

Indo-Malayan connection between eastern Indian and western Pacific Oceans (Rosen, 1984; Fleminger, 1986; Sheppard and Sheppard, 1991). Thus, species richness in these two areas could be in part the product of a sea-level-driven diversity pump (Rosen, 1984). Additional, smaller-scale vicariant separations could have occurred within the complex maze of islands and basins in Indo-Malaya (McManus, 1985).

Although no such regression-associated land barriers are apparent in the insular Pacific, vicariance by extinction of intermediate populations is conceivable and could be driven by sea-level fluctuations. If inner-reef specialists find habitat-related refugia in widely separated areas, then regressions will lead to the fragmentation of their ranges. Such refugia are most likely in the western Pacific (Melanesia, Indo-Malaya, etc.) and on a few, unusual central Pacific islands with reef systems that are minimally disrupted by regressions (*e.g.* Marquesas, Rapa; Paulay, 1990). The relatively high proportion of endemics in the Marquesan and Rapan faunas (Rehder, 1968; Richard, 1984; Randall, 1985) could reflect this process of speciation.

Numerous species that are distributed widely among the islands of Polynesia and Micronesia are nonetheless restricted to the Pacific Plate. To explain the apparent paradox of these widespread Pacific Plate endemics, Springer and Williams (1990) invoked vicariance. Observing that the sister species of several Pacific Plate endemics are restricted to the Indian Ocean, the authors proposed that there previously existed intermediate populations - in the

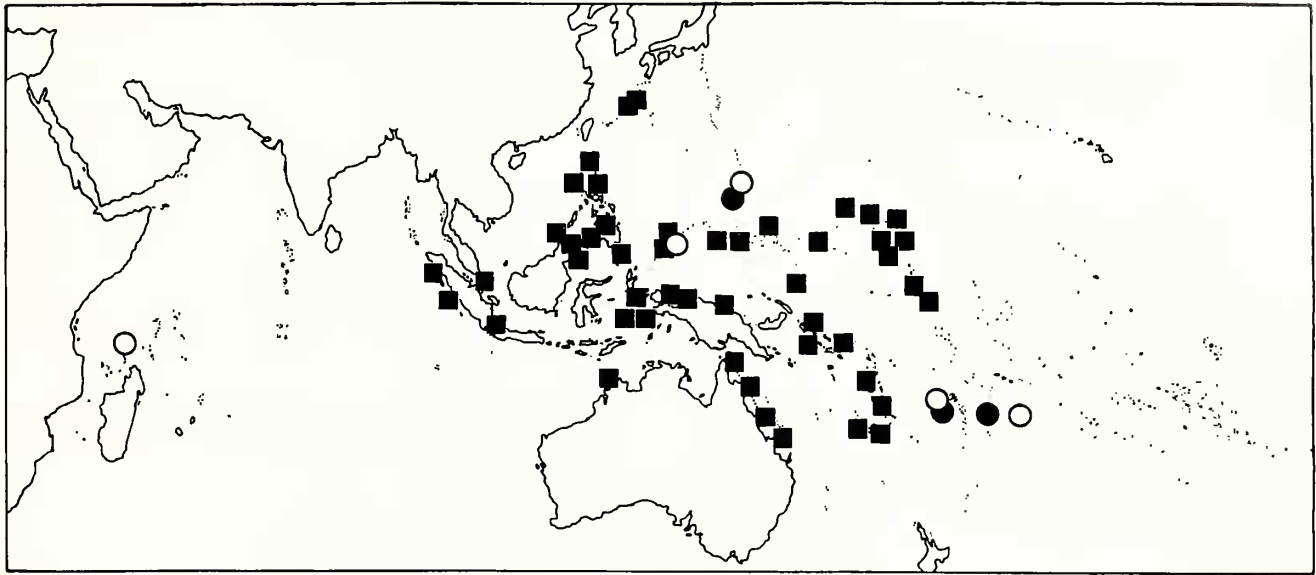


Fig. 7. Present and past distribution of *Hippopus hippopus*. Based on this study and literature records from Rosewater (1965), Taylor (1978), and Lewis *et al.* (1988). (Squares, extant records; solid circles, Holocene records, but presumed extinct; empty circles, Plio-Pleistocene records).

western Pacific Ocean - that have since gone extinct. They hypothesized that the extinction was caused by cooling through increased upwelling and by regression-caused emergence in the area. Indeed, habitat loss due to glacial regressions was high on the large continental shelves of western Indonesia. However, other parts of the western Pacific (*e. g.* the Philippines, Moluccas, Melanesia) were no more affected by habitat loss than central Pacific islands (Myers, 1989), and in fact likely served as habitat refuges for numerous inner-reef-specialist species (Paulay, 1990). Further, although areas of Indo-Malaya could have experienced cooling during glacial times due to increased rates of upwelling (Fleminger, 1986), there is no evidence that Melanesia or the Philippine region were similarly affected. Thus the absence of widespread Pacific endemics from areas like Melanesia and the Philippines is not well-explained by Springer and Williams' (1990) hypothesis.

A purely ecological hypothesis might best explain the phenomenon of widespread Pacific Plate endemics. Organisms that require oceanic marine conditions will thrive in the central Pacific but might not survive in the western Pacific, where large islands - with substantial terrigenous sedimentary and nutrient input - predominate. Abbott (1960) and George (1974) recognized that a significant number of species in the Indo-West Pacific are restricted to areas that are oceanic in character (and others to areas that are continental). Ecological restriction to oceanic conditions could explain not only widespread Pacific endemics, but also other taxa that exhibit disjunct distributions

between oceanic areas of the Pacific and Indian Oceans. A similar ecological hypothesis has been invoked to explain why certain land crab and sea bird species occur to the west and east of, but not in, Indo-Malaya: mammalian predators, absent from most oceanic islands, prevent these species from establishing in the continental area (Indo-Malaya) (Hartnoll, 1988; Steadman, 1989; Paulay, 1994).

Finally, sea-level fluctuations could influence the likelihood of speciation on isolated Pacific islands by affecting the persistence of insular populations. The short-lived populations of inner-reef specialists might not have sufficient time to differentiate into endemics, especially when compared to the long-lived populations of outer-reef inhabitants. I have previously shown (Paulay, 1990) that endemics are significantly more common among outer-reef inhabitants than among inner-reef specialists on central Pacific islands. A corollary to this hypothesis is that inter-island, intraspecific geographic differentiation is expected to be more prevalent and of greater magnitude among outer-reef inhabitants than among inner-reef specialists. No comprehensive database is presently available to test these ideas, but the prevalence of geographic variation in outerreef inhabitants is striking. Examples include species/subspecies complexes of the turbinid *Astrarium rhodostoma* (Lamarck, 1822), the mytilids *Septifer cumingi* Récluz, 1849, and *Septifer furcillata* Gould, 1861, the cardiid *Vasticardium orbita* (Broderip and Sowerby, 1833), the limid *Lima vulgaris*, and the venerid *Dorisca cookei* Dall, Bartsch and Rehder, 1938 (Paulay, unpub.; J. Vidal, pers. comm.).

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LITERATURE CITED

- Abbott, R. T. 1960. The genus *Strombus* in the Indo-Pacific. *Indo-Pacific Mollusca* 1:33-146.
- Abrard, R. 1940. Mollusques Pleistocenes de la côte française des Somalis, recueillis par E. Aubert de la Rue. *Archives du Muséum National d'Histoire Naturelle, 6e série* 18:1-105.
- Aharon, P., S. L. Goldstein, C. W. Wheeler, and G. Jacobson. 1993. Sea-level events in the South Pacific linked with the Messinian salinity crisis. *Geology* 21:771-775.
- Bennett, K. D. 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* 16:11-21.
- Boss, K. J. 1982. Mollusca. In: *Synopsis and Classification of Living Organisms*, S. P. Parker, ed. pp. 945-1166. McGraw-Hill, New York.
- Cernohorsky, W. O. 1970. The littoral marine molluscs of Niue Island. *Records of the Auckland Institute and Museum, 3rd series* 7:175-186.
- Chevalier, J. P. 1979. La faune corallienne (Scleractiniaires et Hydrocoralliaires) de la Polynésie française. *Cahiers de l'Indo-Pacifique* 1:129-151.
- Crame, J. A. 1986. Late Pleistocene molluscan assemblages from the coral reefs of the Kenya coast. *Coral Reefs* 4:183-196.
- Darwin, C. 1842. *The Structure and Distribution of Coral Reefs*. Smith, Elder, London. 214 pp.
- Dautzenberg, P. 1929. Mollusques testacés marins de Madagascar. *Faune des Colonies Françaises, Société d'Éditions* 3:321-636.
- Davis, M. B. 1981. Quaternary history and stability of forest communities. In: *Forest Succession: Concepts and Applications*, D. C. West, H. H. Shugart, and D. B. Botkin, eds. pp. 132-153. Springer-Verlag, New York.
- Dubois J., J. Launay, and J. Recy. 1975. Some new evidence on lithospheric bulges close to island arcs. *Tectonophysics* 26:189-196.
- Fleminger, A. 1986. The Pleistocene equatorial barrier between the Indian and Pacific Oceans and a likely cause for Wallace's line. In: *Pelagic Biogeography*, A. C. Pierrot-Bults, S. van der Spoel, B. J. Zahuranec, and R. K. Johnson, eds. pp. 84-97. UNESCO Technical Papers in Marine Science 49.
- George, R. W. 1974. Coral reefs and rock lobster ecology in the Indo-West Pacific region. *Proceedings of the Second International Coral Reef Symposium, Brisbane* 1:321-325.
- Grigg, R. W. 1982. Darwin point: a threshold for atoll formation. *Coral Reefs* 1:29-34.
- Hartnoll, R. G. 1988. Evolution, systematics, and geographical distribution. In: *Biology of Land Crabs*, W. W. Burggren and B. R. McMahon, eds. pp. 6-54. Cambridge University Press, Cambridge.
- Hirschberger, W. 1980. Tridacnid stocks on Helen Reef, Palau, western Caroline Islands. *Marine Fisheries Review* Feb. 1980:8-15.
- Kay, E. A. 1979. *Hawaiian Marine Shells. Reef and Shore Fauna of Hawaii. Section 4: Mollusca*. Bishop Museum Press, Honolulu. xviii + 653 pp.
- Kilburn, R. N. 1983. The Recent Arcidae (Mollusca: Bivalvia) of southern Africa and Mozambique. *Annals of the Natal Museum* 25:511-548.
- Kosuge, S. 1969. Fossil mollusks from Oahu, Hawaii Islands. *Bulletin of the National Science Museum, Tokyo* 12:783-794.
- Lamy, E. 1937. Révision des Mytilidae vivants du Muséum National d'Histoire Naturelle de Paris. *Journal de Conchyliologie* 81:99-132, 169-197.
- Lewis, A. D., T. J. H. Adams, and E. Ledua. 1988. Fiji's giant clam stocks - a review of their distribution, abundance, exploitation and management. In: *Giant Clams in Asia and the Pacific*, J. W. Copland and J. S. Lucas, eds. pp. 66-72. Australian Centre for International Agricultural Research, Canberra.
- McManus, J. W. 1985. Marine speciation, tectonics and sea-level changes in southeast Asia. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 4:133-138.
- McNutt, M. and H. W. Menard. 1978. Lithospheric flexure and uplifted atolls. *Journal of Geophysical Research* 83:1206-1212.
- Montaggioni, L. F. 1985. Makatea Island, Tuamotu Archipelago. French Polynesia coral reefs: reef knowledge and field guides. *Fifth International Coral Reef Congress, Tahiti* 1:103-157.
- Myers, R. F. 1989. *Micronesian Reef Fishes*. Coral Graphics, Guam. vi + 298 pp., 144 pls.
- Newton, R. B. 1900. Pleistocene shells from the raised beach deposits of the Red Sea. *Geological Magazine, n. s.* 7:500-514, 544-560.
- New Zealand Map Service (NZMS). 1985. *Map of Niue, New Zealand Map Service 250*. Department of Land and Surveys, New Zealand.
- Paulay, G. 1987. Biology of Cook Islands' bivalves, Part I. Heterodont families. *Atoll Research Bulletin* 298:1-31.
- Paulay, G. 1990. Effects of Late Cenozoic sea-level fluctuations on the bivalve faunas of tropical oceanic islands. *Paleobiology* 16:415-434.
- Paulay, G. 1991. Late Cenozoic sea level fluctuations and the diversity and species composition of insular shallow water marine faunas. In: *The Unity of Evolutionary Biology. The Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*, E. C. Dudley, ed. pp. 184-193. Dioscorides, Portland, Oregon.
- Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. *American Zoologist* 34:134-144.
- Paulay, G. 1996. New records and synonymies of Hawaiian bivalves. *Occasional Papers of the Bishop Museum* 45:18-29.
- Paulay, G. and L. R. McEdward. 1990. A simulation model of island reef morphology: the effects of sea level fluctuations, growth, subsidence and erosion. *Coral Reefs* 9:51-62.
- Paulay, G. and T. Spencer. 1988. Geomorphology, palaeoenvironments and faunal turnover, Henderson Island, S.E. Polynesia. *Proceedings of the Sixth International Coral Reef Symposium, Townsville* 3:461-466.
- Paulay, G. and T. Spencer. 1992. Niue Island: geologic and faunatic [sic] history of a Pliocene Atoll. *Pacific Science Association Information Bulletin* 44:21-23.
- Pirazzoli, P. A. and L. F. Montaggioni. 1985. Lithospheric deformation in French Polynesia (Pacific Ocean) as deduced from Quaternary shorelines. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 3:195-200.

- Prashad, B. 1932. The Lamellibranchia of the Siboga Expedition. Systematic part II Pelecypoda (exclusive of the Pectinidae). *Siboga Expedition Reports, Monograph* 53C:1-353.
- Price, C. M. and J. O. Fagolimum. 1988. Reintroduction of giant clams to Yap State, Federated States of Micronesia. In: *Giant Clams in Asia and the Pacific*, J. W. Copland and J. S. Lucas, eds. pp. 41-46. Australian Centre for International Agricultural Research, Canberra.
- Randall, J. E. 1985. Fishes. French Polynesian coral reefs: reef knowledge and field guides: fauna and flora; a first compendium of French Polynesian sea-dwellers. *Fifth International Coral Reef Congress, Tahiti* 1:462-481.
- Rehder, H. A. 1968. The marine molluscan fauna of the Marquesas Islands. *Annual Reports for 1968 of the American Malacological Union*, pp. 29-32.
- Richard, G. 1984. Rapa la méconnue. *Xenophora* 24:7-16.
- Rosen, B. R. 1984. Reef coral biogeography and climate through the Late Cainozoic: just islands in the sun or a critical pattern of islands? In: *Fossils and Climate*, P. Brenchley, ed. pp. 201-262. John Wiley and Sons Ltd., New York.
- Rosewater, J. 1965. The family Tridacnidae in the Indo-Pacific. *Indo-Pacific Mollusca* 1:347-396.
- Salvat, B. 1967. Importance de la faune malacologique dans les atolls polynésiens. *Cahiers Pacifique* 11:7-49.
- Schofield, J. C. 1959. The geology and hydrology of Niue Island, South Pacific. *New Zealand Geological Survey Bulletin, n.s.* 62: 28 pp.
- Sheppard, C. R. C. and A. L. S. Sheppard. 1991. *Corals and Coral Communities of Saudi Arabia*. Fauna of Saudi Arabia 12. 170 pp.
- Simpson, G. G. 1953. *The Major Features of Evolution*. Columbia University Press, New York. xx + 434 pp.
- Spencer, T. and G. Paulay. 1989. Geology and geomorphology of Henderson Island. *Atoll Research Bulletin* 323:1-50.
- Spencer, T., D. R. Stoddart, and C. D. Woodroffe. 1987. Island uplift and lithospheric flexure: observations and cautions from the South Pacific. *Zeitschrift für Geomorphologie, N. F., Supplement-Band* 63:87-102.
- Springer, V. G. 1982. Pacific plate biogeography, with special reference to shorefishes. *Smithsonian Contributions to Zoology* 367:iv + 182 pp.
- Springer, V. G. and J. T. Williams. 1990. Widely distributed Pacific plate endemics and lowered sea-level. *Bulletin of Marine Science* 47:631-640.
- Stanley, S. M. 1979. *Macroevolution*. W. H. Freeman, San Francisco. xi + 332 pp.
- Stanley, S. M., W. O. Addicott, and K. Chinzei. 1980. Lyellian curves in paleontology: possibilities and limitations. *Geology* 8:422-426.
- Steadman, D. W. 1989. Extinction of birds in eastern Polynesia: a review of the record, and comparisons with other Pacific island groups. *Journal of Archaeological Science* 16:177-205.
- Stoddart, D. R. 1973. Coral reefs: the last two million years. *Geography* 58:313-323.
- Taylor, J. D. 1978. Faunal response to the instability of reef habitats: Pleistocene molluscan assemblages of Aldabra atoll. *Palaeontology* 21:1-30.
- Waller, T. R. 1990. The evolution of ligament systems in the Bivalvia. In: *The Bivalvia - Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986*, B. Morton, ed. pp. 49-71. Hong Kong University Press, Hong Kong.
- Webb, T., III. 1987. The appearance and disappearance of major vegetational assemblages: long-term vegetational dynamics in eastern North America. *Vegetatio* 69:177-187.
- Wheeler, C. W. and P. Aharon. 1991. Mid-oceanic carbonate platforms as oceanic dipsticks: examples from the Pacific. *Coral Reefs* 10:101-114.

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